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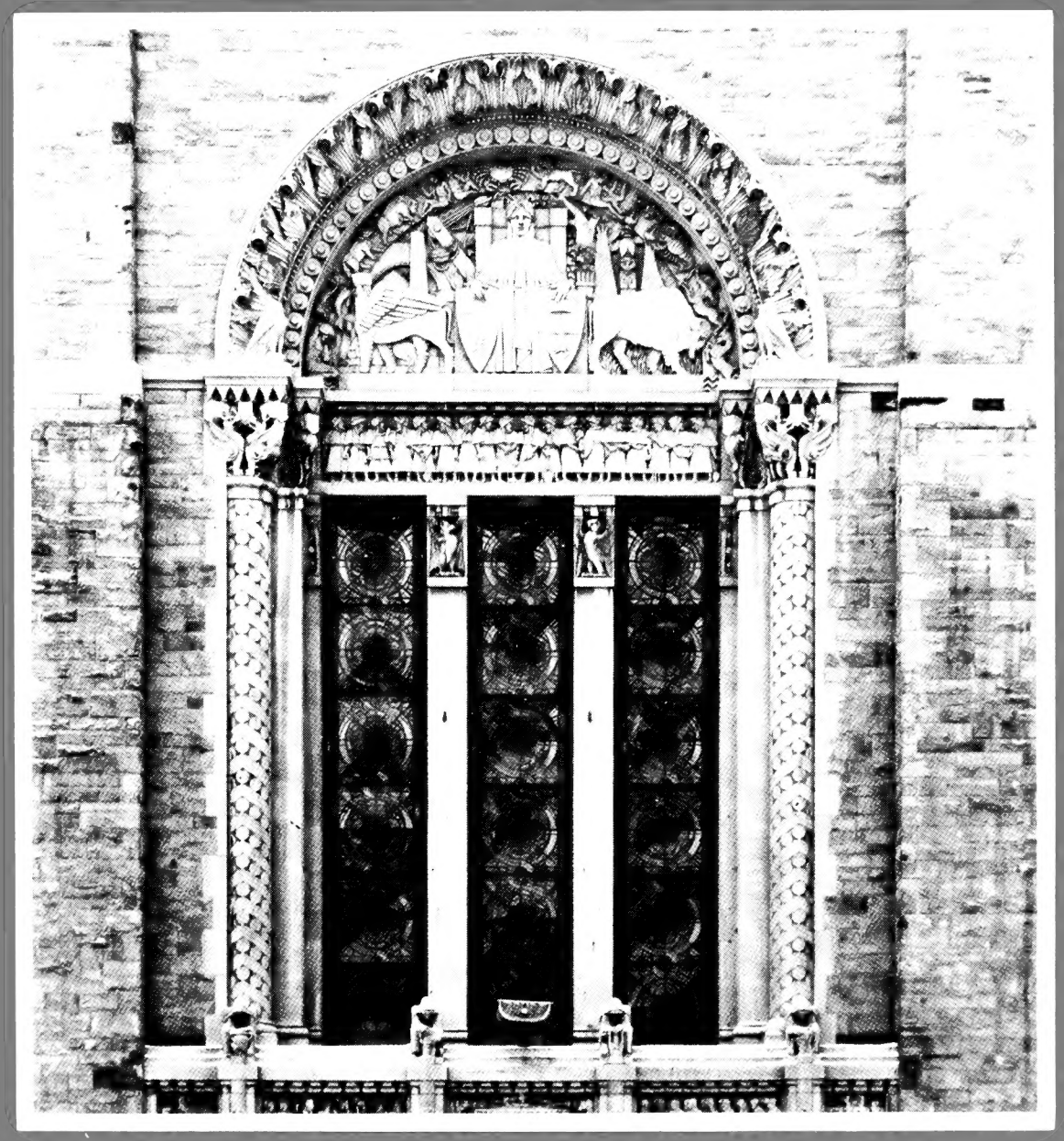

Taxonomy and Palaeoecology of the Silurian Myelodactylid Crinoid *Crinobrachiatus brachiatus* (Hall)

James D. Eckert
and
Carlton E. Brett

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Abstract

Discovery of well-preserved specimens of the fossil myelodactylid crinoid *Crinobrachiatus brachiatus* (Hall) permits detailed description of this genus for the first time. The presence of an aniradial plate, possibly derived from fusion of C-ray inferradial and superradial plates, may indicate derivation from the Iocrinidae. In life, the specialized column could be tightly coiled to partly enclose the crown in a loose baffle formed by unique, branching cirri. These cirri may have served as props to support the column in a semi-recumbent position on the substrate.

Introduction

The Upper Silurian Rochester Formation of western New York and southern Ontario contains a diverse fauna of pelmatozoan echinoderms (Hall, 1852; Springer, 1920, 1926; Brett, 1978a, b). Among these is the myelodactylid crinoid *Crinobrachiatus*, a disparid inadunate characterized by a doubly recurved and coiled stem that bears specialized branching cirri. Occurrence of *Crinobrachiatus* is restricted to the Rochester Formation, where it is represented solely by the type-species *C. brachiatus* (Hall). The distinctive columnals and pluricolumnals of this species are common fossils in the Rochester Formation. The crown of *Crinobrachiatus*, however, is rarely preserved intact. The original description of *Crinobrachiatus* was based on specimens without preserved crowns (Hall, 1852). A collection of 35 specimens obtained at Lockport, New York, possesses only one individual with an intact crown (Springer, 1926). Springer noted that the crown had a general resemblance to *Iocrinus*, but was unable to make out details of its structure. Consequently, taxonomy of *Crinobrachiatus* has been based solely on features of the column and cirri. In this paper, the morphology of the crown of *Crinobrachiatus* is documented for the first time, based on a well-preserved specimen obtained at Lockport. *Crinobrachiatus* is shown to possess features that suggest derivation from the Iocrinidae.

We recommend that classification of the Myelodactylidae be based primarily on morphology of the crown, as the specialized stem and cirri of these genera are potentially homeomorphic features.

Crinobrachiatus brachiatus was a sessile pelmatozoan that was adapted primarily to rather quiet water settings.

Occurrence

Crinobrachiatus is restricted in occurrence to mudstone, calcareous shale, and argillaceous limestone of the lower Rochester Formation in western New York and southern Ontario (Lewiston Member of Brett, 1983). It is commonly associated with small biostromes of ramose bryozoans dominated by *Chilotrypa*, *Hallopora*, and *Trematopora*. In these biostromes, *Crinobrachiatus* is a minor constituent of a diverse echinoderm fauna typically

dominated by *Caryocrinites* and *Stephanocrinus*.

Recently, a specimen of *Crinobrachiatus* with intact crown was collected from a small outcrop in the west branch of Eighteen-Mile Creek at Lockport, New York. This individual (ROM 43049) was derived from a thin biostratigraphic interval designated as the *Homocrinus* beds (Ringueberg, 1888). Frederick Braun, employed by Frank Springer, quarried this layer in 1910, 1911, and 1914, and obtained the only other specimen of *Crinobrachiatus* with an intact crown (USNM S2101). This occurrence of *Crinobrachiatus* is atypical in that it is dominated by the brachiopod *Striispirifer niagarensis* and the small inadunate crinoid *Homocrinus parvus*.

Additional specimens of *Crinobrachiatus* were obtained at Middleport, New York, and two localities in the Niagara Peninsula in southern Ontario. Precise locality information is given in the Appendix.

Systematic Palaeontology

REPOSITORIES

The illustrated specimens are in the collections of the Department of Invertebrate Palaeontology, Royal Ontario Museum (ROM) and the United States National Museum (USNM).

Subclass Inadunata Wachsmuth and Springer, 1885
Order Disparida Moore and Laudon, 1943
Superfamily Myelodactyloidea S. A. Miller, 1883
Family Myelodactylidae S. A. Miller, 1883

DISCUSSION

Classification of the Myelodactylidae differs from that of most crinoids in that this family is characterized by a specialized stem considered to be an important taxobase. The Myelodactylidae constitute the only family of crinoids originally defined on characteristics of the column alone (Miller, 1883). However, the Mississippian camerate genus *Camptocrinus* possesses a specialized stem resembling that of the Myelodactylidae (Springer, 1926; Van Sant and Lane, 1964). Apparently, selection pressure favoured convergent evolution in unrelated crinoids, resulting in homeomorphy of the stem. Homeomorphic tendencies of pelmatozoan stems suggests that classification of the Myelodactylidae should not be based primarily on characteristics of the stem and cirri. Unfortunately, because of nonpreservation of calyces, this is the case in several supposed myelodactylid crinoids including *Brachiocrinus* and *Eomyelodactylus*. Until the crowns of these genera are known, their assignment to the Myelodactylidae must remain tentative. Despite this potential taxonomic pitfall, discovery of calyces in several myelodactylids (*Crinobrachiatus*, *Herpetocrinus*, *Myelodactylus*) suggests that the Myelodactylidae comprise a monophyletic lineage.

Genus *Crinobrachiatus* Moore, 1962

TYPE-SPECIES

Myelodactylus brachiatus Hall, 1852.

DIAGNOSIS

A monotypic genus of Myelodactylidae characterized by a small, conical cup, five pentagonal basals, and five radials, including an undivided C-ray radial (aniradial) supporting an elongate anal tube. Arms five, nonpinnulate, branching isotomously several times. Stem exceptionally varied in diameter, bent in an open S-shaped curve, and bearing numerous stout, branching cirri.

DISCUSSION

Crinobrachiatus is differentiated from other myelodactylids by several characteristics. *Crinobrachiatus* has an undivided rather than a compound C-ray radial, a stem displaying exceptional variation in diameter, and stout, branching cirri instead of the elongate, unbranched cirri characteristic of most myelodactylids.

The lack of intermediate forms inhibits phylogenetic interpretation of *Crinobrachiatus*. Myelodactylids were possibly derived from an iocrinid stock during the Middle or Late Ordovician. Potential ancestors include *Caleidocrinus*, *Iocrinus*, and *Peltacrinus*. However, with the exception of *Peltacrinus*, these genera lack the pentapartite stem characteristic of the proxistele of *Crinobrachiatus*. *Eomyelodactylus* Foerste is presently the oldest known presumed myelodactylid. It occurs in the Lower Silurian Brassfield Formation of Ohio and is of Middle Llandoverian age. *Eomyelodactylus* may represent a root-stock that gave rise to North American myelodactylids.

Whatever the affinities of *Crinobrachiatus*, its unique branching cirri and highly xenomorphic stem are clearly

specialized characteristics not present in other myelodactylids and suggest that the lineage that led to *Crinobrachiatus* was an offshoot that became extinct after the Wenlockian.

Crinobrachiatus brachiatus (Hall, 1852)

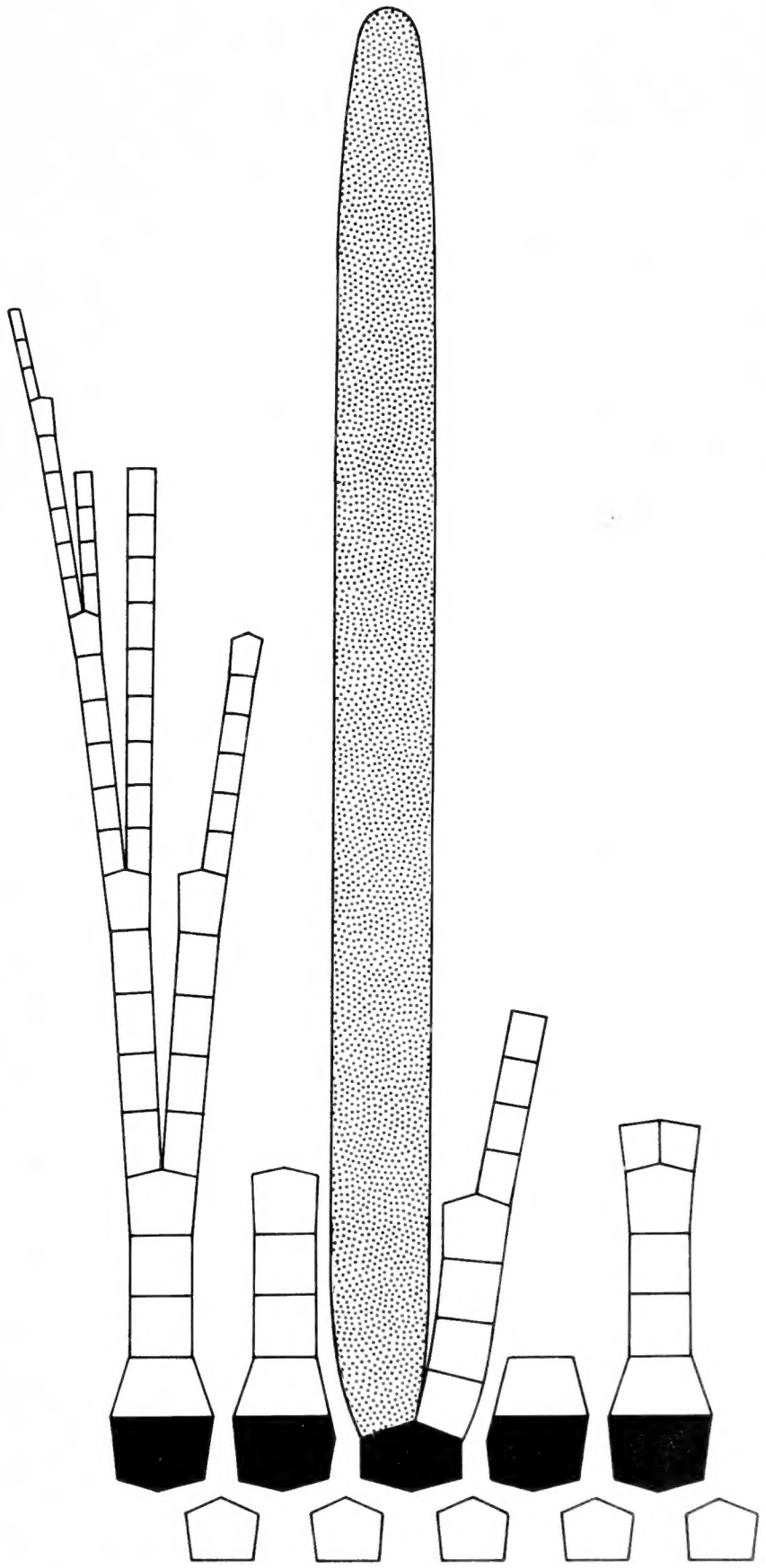
Pls. 1, 2; Text-figs. 1–3

DESCRIPTION

Cup of small size, height and width about 3 mm (ROM 43049), conical with slightly curved walls. Plates of cup smooth, without ornament. Basals five, pentagonal, subequal. Height of basal circlet approximately one-half cup height. A- and E-ray radials larger than basals, five-sided, expanding adorally, height/width ratio approximately 0.8. Posterolateral borders of B- and D-ray radials slightly truncated to accommodate C-ray brachitaxis and anitaxis respectively (Text-fig. 1). C-ray aniradial overlying BC- and CD-interray basals, undivided, hexagonal, slightly wider than high, supporting anal X on oblique, left distal margin and C-ray arm on right facet (Text-fig. 1; Pl. 1, fig. 5). Remaining radial facets plenary, planate.

Arms five, apinnulate, branching isotomously several times. Primibrachials four per ray. First primibrachial of C-ray four-sided, equidimensional, smaller than other first primibrachials. Remaining first primibrachials slightly smaller than underlying radials, trapezoidal, tapering adorally, height/width ratio about 0.6. Second and third primibrachials equidimensional, much narrower than first primibrachials (Pl. 1, fig. 6). Fourth primibrachial slightly elongate, axillary. Secundibrachials five or six per taxis in E-ray arm of ROM 43049. Arms branch again on sixth tertibrachial (Text-fig. 1). Distal portions of arms not preserved. Preserved length of arms 17 mm in ROM 43049. Anal tube narrow, long (19 mm in ROM 43049). Anal X area obscured by pyrite coating in type-specimens. Plates not visible in any portion of anal tube (Pl. 1, figs. 2, 4–6).

Column bilaterally symmetrical and highly xenomorphic with exceptional variation in diameter, ranging from 1 mm immediately below the cup to 6 mm in cirriferous zone; bent in a recurved S-shaped coil that could partly enclose crown (Text-figs. 2, 3; Pl. 1, figs. 1–3). Proxistele comprising one-quarter to one-third of column length, very slender, cylindrical proximally, becoming flattened and ribbonlike distally in plane of coiling (Pl. 2, fig. 1). Proximal columnals low, height/width ratio about 0.2. Distal columnals of proxistele higher, height/width ratio in lateral view about 0.5. Distal columnals of proxistele flattened and elliptical in cross-section, major diameter twice that of minor diameter (Pl. 2, fig. 4). Columnals near U-bend at proxistele-mesistele junction slightly cuneiform. Stem diameter increasing rapidly in mesistele, attaining diameter five or six times that of proxistele. Mesistele curved in broad, open loop, composed of uniformly low, broad columnals, trapezoidal in cross-section. Mesistele columnals flattened to slightly concave on inner surface of curve, strongly convex on outer side (Pl. 2, figs. 2, 4). Articular surfaces of mesistele



Text-fig. 1 Plate diagram of *Crinobrachiatus brachiatus*. Note undivided aniradial in C-ray. Block shading indicates radial plates; stippling indicates anal tube.

columnals bilaterally symmetrical with broad, elliptical lumen surrounded by five shallow, depressed petaloid areas possibly representing ligament fossae (Pl. 2, fig. 4). Three fossae above lumen towards outside of curve; remaining two below and directed towards lower corners of columnal. Crenularium ill defined. Area between the two lower ligament fossae possibly bearing vague vermicular culminae. Dististele composed of trapezoidal columnals proximally and subpentagonal columnals near terminus. Dististele bearing two rows of alternating cirri, one on each side of plane of coiling, located beyond closely coiled portion of column (Pl. 2, fig. 3). Three to nine large, branching cirri present in each row in adult individuals, becoming progressively smaller and more closely spaced distally. Cirri branching several times, giving rise to anteriorly directed spurlike projections (Pl. 1, fig. 7; Pl. 2, fig. 11). Proximal cirri stout, directed obliquely upwards and inwards, covering coiled portion of column (Text-figs. 2, 3), each typically borne by single columnal on lobate, spear-shaped extension (Pl. 2, fig. 13). Adjoining columnals fused together forming this platform in some individuals (ROM 43049; Pl. 1, fig. 6). Distal columnals with cirri lacking these extensions. Distal cirri oriented at nearly right angles to stem. Cirrals stout, blocky, with symplexial sutures (Pl. 2, figs. 5, 9). Dististele tapering gradually, terminating in discoidal or digitate holdfast in some specimens (Pl. 2, figs. 6–8).

DISCUSSION

Although admitting he could not fully determine details of its structure, Springer (1926, pl. 4, fig. 1A; Pl. 1, fig. 1 herein) provided a diagram of the crown of *Crinobrachiatus brachiatus* based on the single specimen then available for study. Examination of this specimen (USNM S2101) by us indicates that Springer's interpretation is in error. Apparently, Springer did not recognize the CD-interray of his specimen and interpreted the poorly preserved anal tube as an arm. This misinterpretation is understandable as the structure is partially obscured by pyrite. However, the undivided C-ray radial (aniradial) is visible when this specimen is immersed in ethanol. We initially thought that the undivided aniradial might be an abnormality since a divided C-ray radial is characteristic of other myelodactylids. However, partial dissection of ROM 43049 revealed that this individual also possesses an undivided C-ray aniradial. This specimen was subsequently reassembled without damage. We consider an undivided aniradial to be characteristic of *Crinobrachiatus*. This plate was possibly derived from fusion of separate C-ray inferradial and superradial ossicles typical of the myelodactylids *Myelodactylus* and *Herpetocrinus*. Why fusion of these plates may have occurred in *Crinobrachiatus* is open to speculation. It may represent a response to the problem of support of the relatively long anal tube. Fusion of C-ray radial plates, also observed in certain calceocrinids, would produce a single larger plate that would strengthen the small cup by spreading stress over a wider area (Brett, 1981a). Alternatively, the C-ray of *Crinobrachiatus* may have been simplified by expulsion of an overlying brachianal from the cup.

Biostratinomy of Crinobrachiatus

The *Homocrinus* beds of the Rochester Formation at Lockport, New York, are noted for well-preserved fossils. Ringueberg (1888:269) observed that "the fine state of preservation of many fossils occurring in this band and the layers immediately above and below is noteworthy. This is especially true of species as a rule found only in disarticulated condition." *Asaphocrinus ornatus*, *Homocrinus parvus*, *Caryocrinites ornatus*, and other echinoderms associated with *Crinobrachiatus* in this unit commonly are completely articulated and possess the entire column and holdfast. Thus, the rarity of *Crinobrachiatus* individuals preserved with the crown intact is somewhat enigmatic. Autotomization is a possible explanation. Springer (1926:18) judged that "this form must have been peculiarily sensistive to disturbance or change of conditions, causing it to cast off the crown, as certain existing crinoids cast off their arms on being brought to the surface."

One specimen of *Crinobrachiatus* with intact crown (ROM 43049, Pl. 1, figs. 3–6) was discovered by splitting a slab of shale. The posterior side of this individual exhibits better preservation than the anterior side. This is indicated by the arms, which are preserved almost to their extremities on the posterior side of the crown (C-, D-, and E-rays), but only to the first secundibrachials on the anterior side (A- and B-rays) (Pl. 1, fig. 6). Furthermore, the stout, branching cirri are represented only by their attachment scars on the anterior side, yet well-preserved cirri were observed on the posterior side during partial dissection of the crown. The tightly coiled stem also shows slight separation of columnals in several places. Associated crinoids in the *Homocrinus* beds show similar features. When this mode of preservation is present, the lower surface of the crown—the side that rested on the seafloor—is invariably better preserved than the upper surface. This suggests that, following dislodgement by

currents, the echinoderms lay partly exposed on the seafloor, where decay aided disarticulation and scattering of ossicles. This process was restricted to exposed upper surfaces as underlying sediment prevented disarticulation of the lower surfaces. Only a brief period of time was involved. Recent experiments show that modern crinoids decay rapidly and disarticulate completely within five to ten days of death (Meyer, 1971; Liddell, 1975). In individuals from the *Homocrinus* beds, the decay process had barely begun before the crinoids were completely buried by an influx of sediment that inhibited further disarticulation.

Functional Morphology

The family Myelodactylidae is characterized by development of specialized cirri on each side of a bilaterally symmetrical, coiled, and recurved column (Springer, 1926; Moore, 1962). Most myelodactylids, including *Herpetocrinus* and *Myelodactylus*, possess closely spaced cirri that are long, slender, and unbranched. In contrast to these crinoids, *Crinobrachiatus* possesses stout, widely spaced, branching cirri. These cirri are unique; in all other pelmatozoans branching cirri, if present, are restricted to distally developed holdfasts. The branching cirri and strongly xenomorphic column of *Crinobrachiatus* suggest that this crinoid had a mode of life unlike that of other myelodactylids. However, the functional morphology and palaeoautecology of *Crinobrachiatus* have not previously been considered in detail (but see Ehrenberg, 1929, 1930a, b; Brett 1981b).

Profuse development of long, slender, unbranched cirri in most myelodactylids presumably had a defensive function, providing a well-developed baffle that could completely enclose the delicate crown. This adaptation may have permitted these crinoids to inhabit higher-energy environments and may account for their widespread distribution in calcarenite and mudstone facies. The unique cirri of *Crinobrachiatus*, in contrast, formed a loose baffle that could only partly conceal the crown. During periods of intense storm activity, the partly exposed crown may have been susceptible to damage. We postulate that *Crinobrachiatus* was primarily adapted to rather quiet-water, muddy settings. At the Lockport occurrence, *Crinobrachiatus* is associated with the minute, fragile inadunate crinoid *Homocrinus parvus*. This occurrence is interpreted to represent a normally quiet-water, mud-bottom community that was disrupted by storm waves or currents (Brett, 1978a).

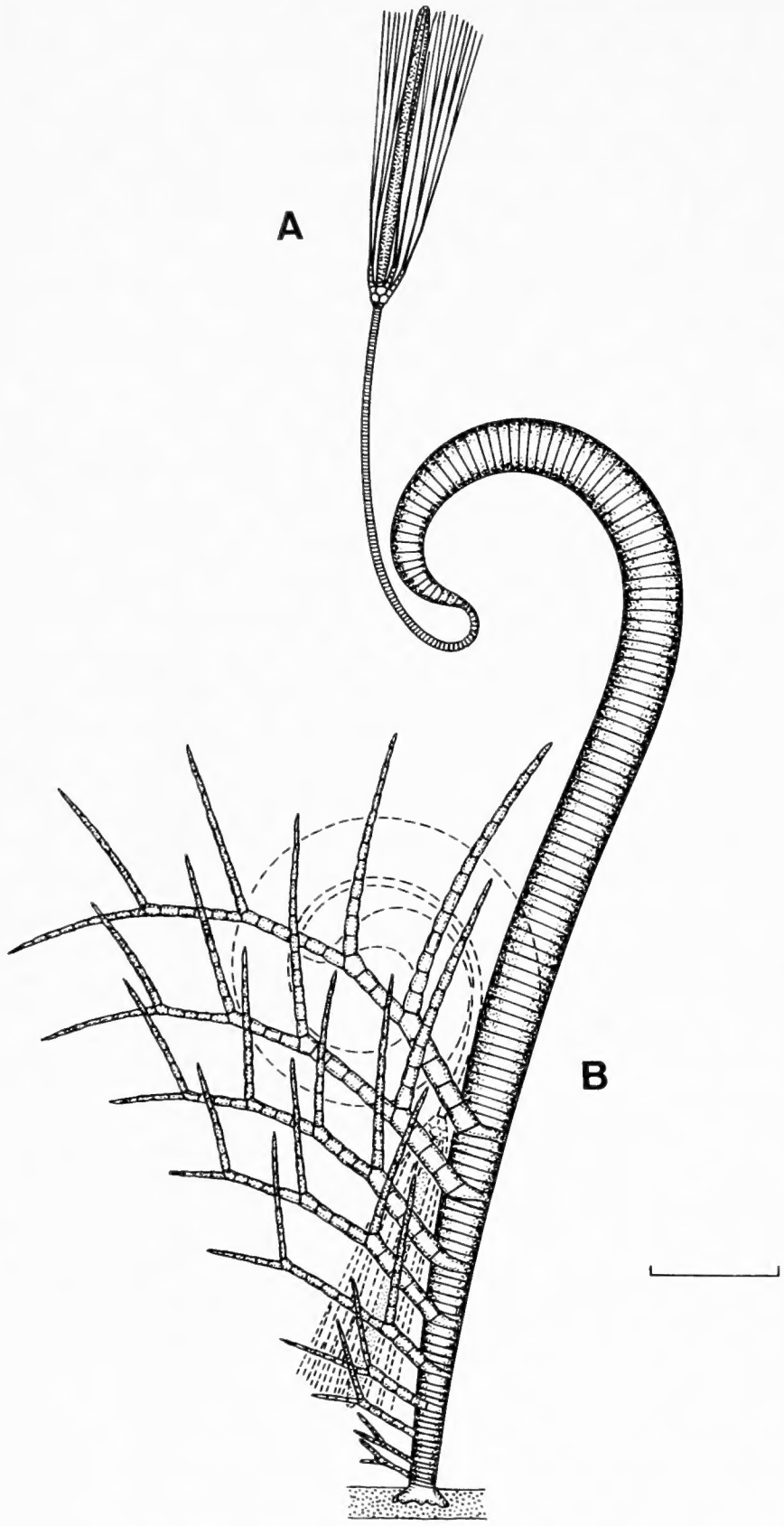
Previous workers (Kirk, 1911; Springer, 1926, pl. 4, fig. 1; Ehrenberg, 1929, 1930a, b) believed that *Crinobrachiatus* lacked a distal holdfast. However, we have discovered both juvenile and adult *Crinobrachiatus* individuals with lobate or digitate holdfasts typically cemented to bryozoans (Pl. 2, figs. 6–8). Common association of *Crinobrachiatus* with bryozoan patches in the Rochester Formation suggests that this crinoid may have selectively colonized these biostromes. This is particularly evident in the Lockport occurrence, where *Crinobrachiatus* occurs selectively with small localized bryozoan patches but not commonly in intervening areas of the same bedding plane.

During early ontogenetic stages, *Crinobrachiatus* probably grew upright as in "normal" crinoids, as indicated by the development of a roughly circular holdfast and radially symmetrical distal-most columnals. Although evidence was lacking, previous investigators have also depicted mature individuals as growing upright (Fenton and Fenton, 1958:130; Text-fig. 2). A recently discovered large *Crinobrachiatus* specimen with a stout, well-developed holdfast may have retained an upright orientation throughout its life (ROM 43056, Pl. 2, fig. 8). This individual is unusual in that it possesses only two or three robust, branching cirri located immediately above the holdfast and directed upwards towards the crown. These cirri may have formed a loose baffle enclosing the crown. Alternatively, distal portions of the cirri may have grasped other objects, providing additional support. However, *Crinobrachiatus* cirri are rather stout and have not been observed coiled around other objects.

Digitate or lobate holdfasts were apparently absent in many mature *Crinobrachiatus* individuals. The stems of these individuals are lined with branching cirri that become shorter and more closely spaced distally (ROM 43053, Pl. 2, fig. 10). The absence of digitate or lobate holdfasts suggests that the lateral cirri had supportive functions. These and other morphological features discussed below lead to the interpretation of a unique, semi-reclined mode of life for many adult individuals.

There are several peculiarities of the *Crinobrachiatus* column and cirri that must be considered in any functional reconstruction: a) medial and distal portions of the column are coiled and bilaterally symmetrical, b) cirri occur in two rows, one on each side of the column, c) cirri are branched and stout, d) cirri length increases progressively towards proximal part of column, and e) proximal column is recurved and lacks cirri.

An evolutionary trend existed within primitive pelmatozoans towards perfection of radially symmetrical columns from irregular polyplated steles or pentameric stalks. Crinoid columns that were vertically oriented in life are



Text-fig. 2 Restoration of *Crinobrachiatus brachiatus* in upright orientation with column partly uncoiled (A), and column fully retracted (B). Cirri are depicted on one side of the column only. Crinoid is shown attached to bryozoan. Scale is 1 cm.

typically composed of radially symmetrical columnals. Lateral cirri, if present, are also radially disposed around the column and are invariably unbranched. This may be adaptively advantageous in providing a streamlined support rod for the crown; water will flow evenly around the symmetrical column, generating a minimum of torque which might tend to dislodge the holdfast. The cirri were probably functional in maintaining balance in upright crinoid columns (Lane, 1968; Haugh, 1978).

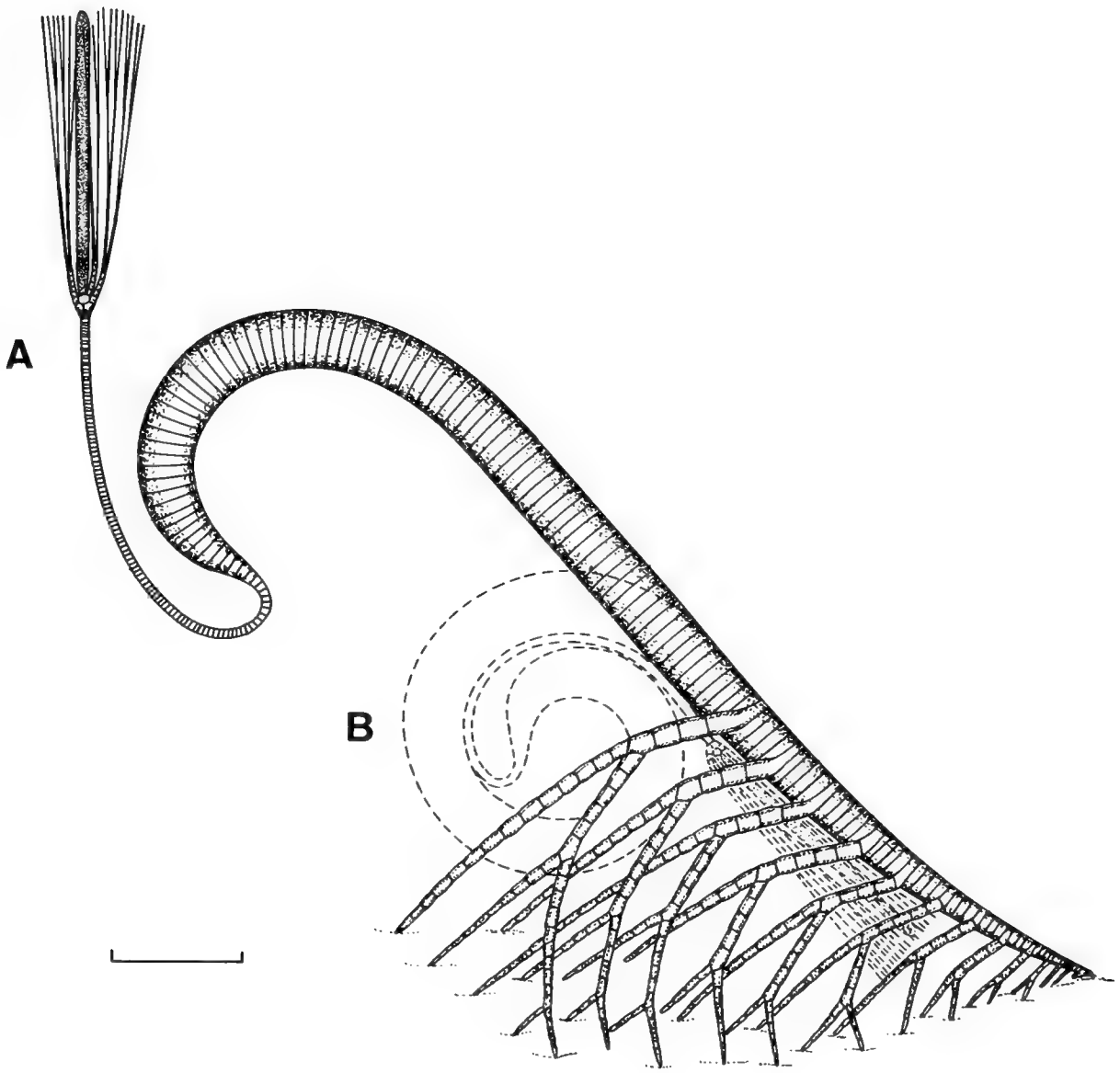
In contrast, distal portions of columns that acted as horizontal creeping holdfasts or stolons are commonly bilaterally symmetrical in cross-section, with the flattened to slightly concave lower surface resting on or directly cemented to the substrate (Franzén, 1977; Brett, 1981b). Stoloniferous holdfasts also commonly possess rows of pseudocirri or radicular cirri, which are symmetrically disposed on either side of the column and are directed downwards and attached to the substrate (Brett, 1981b). The dististele of *Crinobrachiatus* resembles stoloniferous holdfasts in that it is bilaterally symmetrical in cross-section and possesses two rows of cirri. By analogy, we postulate that *Crinobrachiatus* cirri were typically directed downwards towards the seafloor in life orientation, with the dististele directed at an oblique angle to the substrate (Text-fig. 3).

A semi-recumbent orientation for *Crinobrachiatus* is also supported by the morphology of the cirri. The cirri are stout and branched, with most branches directed away from the dististele. Branching cirri are common in pelmatozoans but they are typically associated with distal holdfast areas. Stout, branched, radicular cirri are generally directed downwards at an oblique angle to the main column. They invariably bifurcate towards the substrate rather than away from it. In *Dolatocrinus*, *Gennaeocrinus*, and many other crinoids, branched radicles apparently acted as a prop for the main column. A similar interpretation is made here for *Crinobrachiatus*.

Crinobrachiatus cirri show a regular, progressive increase in length towards the coiled portion of the mesistele. The increase in cirral length is readily interpretable if this crinoid had a semi-recumbent orientation as an adult: such an array of cirri would raise the crown and proxistele above the substrate. Intergrowth of a cirrus of *Crinobrachiatus* with roots of *Caryocrinites* (Pl. 2, fig. 12) indicates that the tips of the cirri rested on the substrate. Short distal cirri would function primarily in anchorage, whereas proximal cirri would serve mainly as struts or stilts (Text-fig. 3).

Extensive development of *Crinobrachiatus* cirri in a column with an upright orientation may have produced a "top-heavy" condition which would have tended to cause the crinoid to topple towards the cirrus-weighted side. Indeed, this may have been the common ontogenetic pattern, assuming that immature *Crinobrachiatus* individuals had an upright orientation.

In order for the crown to be retracted into the coiled mesistele with the semi-recumbent model, it would have to have been rotated to an inverted position obliquely parallel to the substrate (Text-fig. 3). To test whether or not the proposed orientation provides sufficient clearance



Text-fig. 3 Restoration of *Crinobrachiatus brachiatus* in semi-recumbent orientation with column partly uncoiled (A), and column fully retracted (B). Cirri are depicted on one side of column only. Scale is 1 cm.

for the crown to be retracted, we constructed a wire scale model of *Crinobrachiatus*. The model demonstrates that the long proximal cirri would have raised the proximal column sufficiently above the seafloor to allow the crown to clear the substrate during coiling. It is still possible that distal tips of the arms would have dragged across the substrate; however, we do not believe that this would preclude the interpretation of a recumbent orientation. The ambulacra of *Crinobrachiatus* and other crinoids possessed cover plates which could be closed to prevent damage or fouling of the tube feet. Moreover, in calceocrinids, for which a recumbent life-mode is known, closing of the hinged crown brought the arms virtually into contact with the substrate without ill effect.

The coiled column of *Crinobrachiatus* is commonly considered to have been a defensive adaptation coordinated with the evolution of a small, fragile crown. This interpretation appears plausible. However, as indicated previously (p. 7), the cirri of *Crinobrachiatus* could not enclose the crown as effectively as those of other myelodactylids. We believe that the coiled column also served to reduce stresses associated with life in a near-substrate zone. Organisms that live at or close to the sediment-water interface are subject to certain common stresses not shared with high-level suspension-feeding pelmatozoans, most notably burial and fouling by resuspended fine-grained sediments. Most near-substrate organisms possess mechanisms for closure during periods of high turbidity and rapid sedimentation. Examples include bivalved shells and the operculum in the coral *Calceola*. Brett (1981a) postulated that a major function of the calceocrinid hinge was protection from turbidity and burial. Calceocrinids could disinter themselves from thin layers of sediment simply by opening the hinge. Uncoiling of the column in *Crinobrachiatus* could have performed a similar function.

Mesistele columnals of *Crinobrachiatus* possess well-developed articular surfaces and muscle-attachment areas that permitted the column to be readily coiled (Pl. 2, fig. 4). Each mesistele columnal has a trapezoidal cross-

section that reduces its effective radius in the plane of coiling. This characteristic permitted the mesistele to be tightly coiled. Furthermore, the recurved portion of the column is characterized by flattened, ribbonlike columnals that permitted an abrupt change in curvature so that the crown could be partly enclosed within the coil.

In summary, we infer that *Crinobrachiatus* had both upright and semi-recumbent modes of life. Columns of juvenile individuals were probably oriented approximately perpendicular to the substrate. This orientation was retained in some adults with limited development of branching cirri (Text-fig. 2). In many mature individuals, extensive development of cirri shifted the centre of gravity to one side of the column, causing the crinoids to gradually assume a semi-recumbent orientation (Text-fig. 3).

Acknowledgements

Dr Porter M. Kier of the United States National Museum kindly loaned a specimen of *Crinobrachiatus* from the Springer collection. The specimens illustrated on Plate 2 (figs. 7 and 8) were collected by Denis Tetreault and Bea-Yeh Lin, respectively, of the University of Rochester. Preparation facilities and photographic equipment were provided by the Royal Ontario Museum and the University of Rochester. This study benefited from discussion and curatorial services provided by Dr Peter von Bitter, David Rudkin, and Janet Waddington of the Department of Invertebrate Palaeontology at the Royal Ontario Museum. James Brower and James Sprinkle critically reviewed the manuscript.

Appendix

Register of Localities

1. United States Geological Survey (USGS) Medina 7.5′ Quadrangle. Exposure of Rochester Formation in bed of tributary of Jeddo Creek, 0.7 km south of Route 31 and 0.4 km east of Telegraph Road, Niagara County, New York. 43°11′5″ N. Lat., 78°28′19″ W. Long.
2. USGS Lockport 7.5′ Quadrangle. Highly weathered and largely overgrown exposure of Rochester Formation in hill slope just west of Scovell Street and 0.2 km north of intersection of Scovell and Gooding streets, Niagara County, New York. 43°10′38″ N. Lat., 78°41′29″ W. Long.
3. USGS Lockport 7.5′ Quadrangle. Exposure of *Homocrinus* beds of the Rochester Formation in west branch of Eighteen-Mile Creek, 0.25 km east of Route 93 and 1 km north of Route 31, Niagara County, New York. 43°10′15″ N. Lat., 78°43′38″ W. Long.
4. National Topographic Series (NTS) Niagara 30M/3. Rochester Formation formerly exposed in tributary of Dick Creek, 200 m east of Highway 406, St Catharines, Lincoln County, Ontario. Exposure was covered by construction of erosion-resistant barrier in 1984 and is no longer accessible. 43°07′56″ N. Lat., 78°13′26″ W. Long.
5. NTS Niagara 30M/3. Rochester Formation exposed in west bank of Twenty-Mile Creek, 0.6 km south of lower falls at Ball's Falls, Jordan, Lincoln County, Ontario, 43°07′57″ N. Lat., 79°23′04″ W. Long.

Literature Cited

BRETT, C.E.

1978a Systematics and paleoecology of Late Silurian (Wenlockian) pelmatozoan echinoderms from western New York and Ontario. Ph.D. Thesis, University of Michigan. 603 pp.

1978b Host-specific pit-forming epizoans on Silurian crinoids. Lethaia 11:217–232.

1981a Systematics and paleoecology of Late Silurian (Wenlockian) calceocrinid crinoids from western New York and southern Ontario. Journal of Paleontology 55:145–175.

1981b Terminology and functional morphology of attachment structures in pelmatozoan echinoderms. Lethaia 4:343–370.

1983 Sedimentology, facies and depositional environments of the Rochester Shale (Silurian: Wenlockian) in western New York and Ontario. Journal of Sedimentary Petrology 53:947–971.

EHRENBERG, K.

1929 Pelmatozoan root-forms (fixation). Bulletin of the American Museum of Natural History 59:1–76.

1930a Die "Nebenformen" der Crinoiden, ihre stammesgeschichtliche Entwicklung und Bedeutung. Palaeobiologica 3:257–324.

1930b Form und Funktion bei der "Nebenformen" der Crinoiden. Paläontologische Zeitschrift 12:170–177.

FENTON, C.L. and M.A. FENTON

1958 The fossil book. Garden City, N.Y., Doubleday. 482 pp.

FRANZÉN, C.

1977 Crinoid holdfasts from the Silurian of Gotland. Lethaia 10:219–234.

HALL, J.

1852 Palaeontology of New York. Volume 2, containing descriptions of the organic remains of the lower Middle division of the New York System. Albany, printed by C. Van Benthuysen. 362 pp.

HAUGH, B.N.

1978 Biodynamic and phyletic paradigms for sensory organs in camerate crinoids. Lethaia 11:145–173.

KIRK, E.R.

1911 The structure and relationships of certain eleutherozoic pelmatozoa. Proceedings of the United States National Museum 41:1–137.

LANE, N.G.

1968 The adaptive significance of balance in Paleozoic stalked crinoids. Geological Society of America, Abstracts for 1968 (GSA Special Paper 121):169. [Abstract]

LIDDELL, W.D.

1975 Recent crinoid biostratinomy. Geological Society of America, Abstracts with Programs 7:1169. [Abstract]

MEYER, D.L.

1971 Post-mortem disarticulation of recent crinoids and ophiuroids. Geological Society of America, Abstracts with Programs 3:645. [Abstract]

MILLER, S.A.

1883 Echinodermata. *In* The American Palaeozoic fossils, Cincinnati, private publication, S.A. Miller, pp. 276–288.

MOORE, R.C.

1962 Ray structure of some inadunate crinoids. University of Kansas Paleontological Contributions, Echinodermata, Article 5:1–47.

MOORE, R.C. and L.R. LAUDON

1943 Evolution and classification of Paleozoic crinoids. Geological Society of America, Special Paper 46:1–153.

RINGUEBERG, E.N.S.

1888 The Niagara Shales of western New York. American Geologist 1:264–272.

SPRINGER, F.

1920 The Crinoidea Flexibilia. Smithsonian Institution Publication 2501:1–443.

1926 Unusual forms of fossil crinoids. Proceedings of the United States National Museum 67, Article 9:1–137.

VAN SANT, J.F. and N. LANE

1964 Crawfordsville (Indiana) crinoid studies. University of Kansas Paleontological Contributions, Echinodermata, Article 7:1–136.

WACHSMUTH, C. and F. SPRINGER

1885 Revisions of the Palaeocrinoidea. Proceedings of the Academy of Natural Sciences of Philadelphia for 1885:225–364.

Plate 1, figs. 1–7

Crinobrachiatus brachiatus (Hall). Rochester Formation, western New York and southern Ontario.

1. Partly coiled individual with crown and most of the highly xenomorphic stem. This specimen was figured by Springer (1926, pl. 4, fig. 1) and Moore (1962, pl. 3, fig. 2a). USNM S2101, × 2.4, locality 3.

2. CD-interray of crown of above individual. Proximal portion of the anal tube is visible. USNM S2101, × 10.5.

3. Specimen with well-preserved crown, showing column in fully retracted position. In life, the crown was partly concealed by branching cirri, not shown in this individual. ROM 43049, × 3.3, locality 3.

4. Distal portion of anal tube preserved on counterpart of above individual. ROM 43049a, × 6.1.

5. CD-interradius of ROM 43049, × 6.7. Note undivided aniradial in C-ray.

6. Crown of ROM 43049, × 6.7, centred on A-ray. The isotomously branching arms are preserved nearly to their extremities in the D-ray. Proximal portion of the anal tube is visible. Attachment sites for three cirri are preserved on the column. This specimen displays the exceptional variation in diameter of the stem that is typical of this species.

7. Large individual with missing crown, showing typical preservation. The stout, branching cirri are well preserved. ROM 43050, × 1.8, locality 5.

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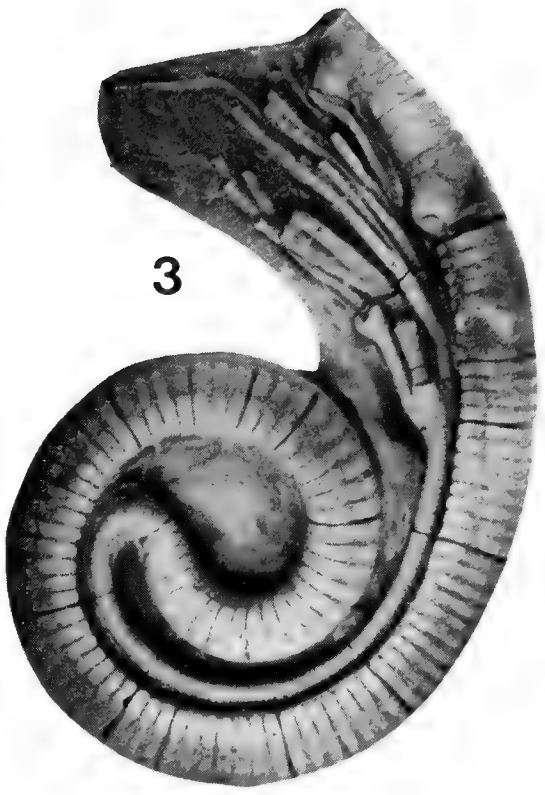

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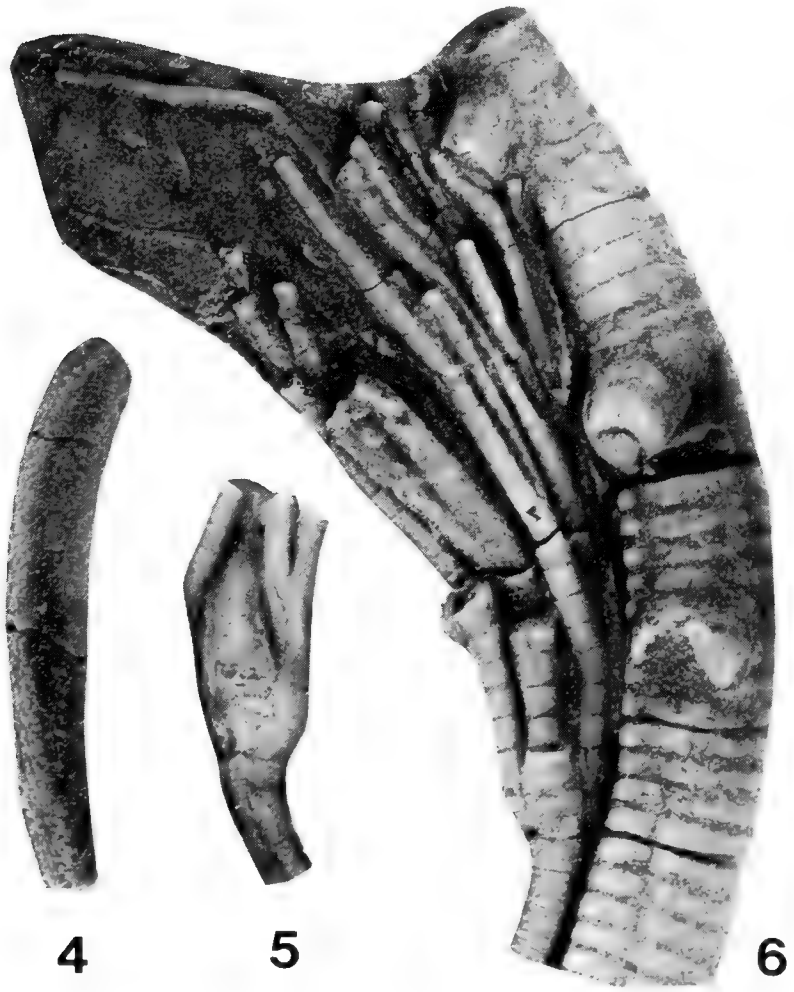

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Plate 2, figs. 1–13

Crinobrachiatus brachiatus (Hall). Rochester Formation, western New York and southern Ontario.

1. Pluricolumnal seen from inner side of coil. The narrow, proximal portion of the proxistele is resting on the much larger mesistele. (See also Pl. 2, fig. 4.) ROM 43049, × 3, locality 3.

2. Pluricolumnal seen from outer side of coil, showing gaps between columnals. ROM 43050, × 3.3, locality 5.

3. Pluricolumnal seen from outer side of coil, showing alternate arrangement of cirri. ROM 43050, × 3.8, locality 5.

4. Transverse section through mesistele (top) and proxistele. Individual pentameres can be seen in the proxistele. A narrow, elliptical lumen is visible in the mesistele and is apparently bisected by a ligament fossa. ROM 43049, × 6.5, locality 3.

5. Articular surface of cirral. ROM 43055, × 12, locality 2.

6. Nearly complete juvenile individual with holdfast and disarticulated calyx. ROM 43051, × 6.8, locality 3.

7. Nearly complete juvenile individual attached to fragment of trepostome bryozoan. ROM 43052, × 5.5, locality 1.

8. Large individual with well-developed holdfast attached to fragment of trepostome bryozoan. ROM 43056,× 1.7, locality 1.

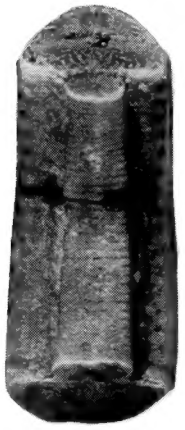
9. Part of cirrus with slightly depressed cirral sutures. ROM 43050, × 8, locality 5.

10. Specimen attached to foliate zoarium of *Lichenalia*. A trepostome bryozoan is also present. ROM 43053, × 3.2, locality 1.

11. Typical specimen with partial preservation of branching cirri. ROM 43054, × 1.7, locality 4.

12. Lower right area of above with intergrowth of *Caryocrinites* radicle and cirrus of *Crinobrachiatus*. ROM 43054, × 6.3.

13. Pluricolumnal from mesistele with attachment areas for two cirri. Note partial fusion of columnals. ROM 43054, × 6.4, locality 4.



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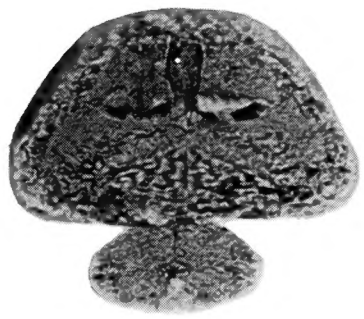

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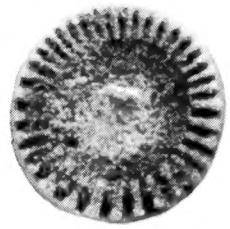

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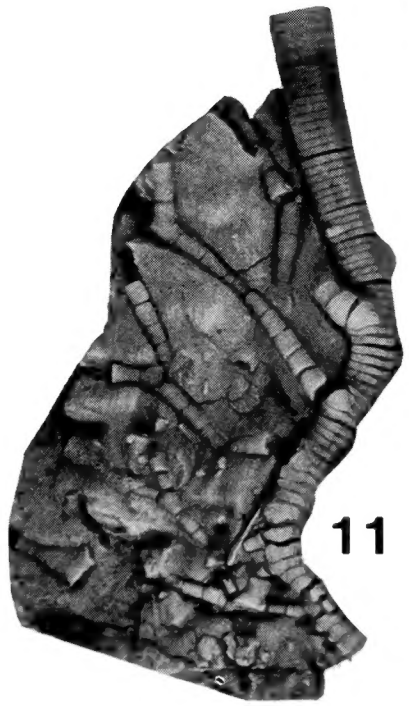

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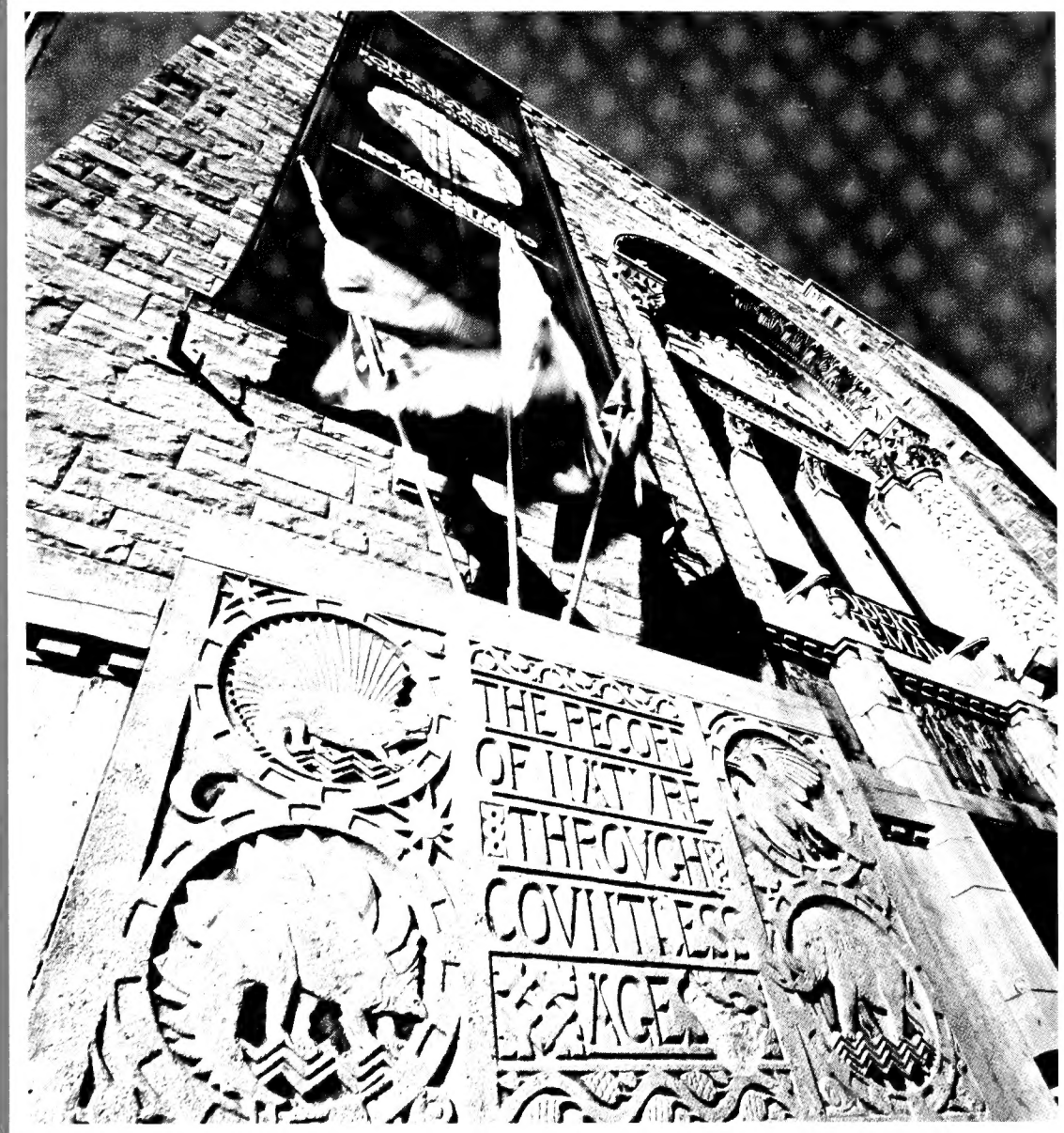

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